PROC. BIOL. SOC. WASH.
107(1), 1994, pp. 164–173

NEW SPECIES OF *MARIONINA* (ANNELIDA: OLIGOCHAETA: ENCHYTRAEIDAE) FROM *SPARTINA* SALT MARSHES ON SAPELO ISLAND, GEORGIA, U.S.A.

Brenda Healy

Abstract.—Three new species of *Marionina* are described from *Spartina* salt marshes where they were associated with live and dead *Spartina* stems. All three species appear to be confined to this habitat. *Marionina spartinae* is distinguished by paired sigmoid setae, an anteclitellar origin of the dorsal vessel and elongated sperm bundles in the spermatheca. *Marionina waltersi* has 2–3 sigmoid setae per bundle, a long, narrow sperm funnel and a poorly developed seminal vesicle. *Marionina paludis* resembles *M. appendiculata* in having fan-like bundles of 3–6 sigmoid setae but differs in its larger sperm funnel and well developed seminal vesicle and the presence of a compact penial bulb. These are the first records of Enchytraeidae from the marine littoral zone of Georgia.

There have been few studies of marine littoral Enchytraeidae in the east of North America. Published records concern only the northern United States from Maine to South Carolina (Moore 1905, Welch 1917, Lasserre 1971) or Bermuda (Moore 1902, Lasserre & Erséus 1976, Giere 1979). With the exception of a single record of *Stephensoniella marina* (Moore, 1902) (Coates 1983) and some preliminary data from West Florida (Healy 1989), there is no information from more southern states. The new species described in this paper are thus the first records of *Marionina* from the southern Atlantic coast.

Sparina salt marshes, with *S. alterniflora* Loisel, 1907 (smooth cordgrass) the dominant species, cover extensive areas of the intertidal zone from Canada to mid-Florida (where they are replaced by mangroves) and on the Gulf coast as far as Texas (Reimold 1977). On the coast of Georgia, they form a belt approximately 7 km wide and the plants here grow luxuriantly, reaching 2–3 m in height with a basal diameter of 3 cm on the banks of creeks (Wiegert et al. 1981). There is extensive literature on many aspects of the Sapelo Island marshes, including their invertebrate fauna, but while oligochaetes have been shown to be an important component of the fauna of the marsh surface (Teal 1962), they have not, so far, been identified, even to family.

Preliminary investigations of salt marsh oligochaetes on the Sapelo marshes showed that Tubificidae and Enchytraeidae were present on the marsh surface, mainly in plant debris, but that both were far more abundant in the lower regions of *Spartina* stems. The three new species described in this paper, together with another enchytraeid, *Marionina appendiculata* Nielsen & Christensen, 1959 and a tubificid, *Monopylephorus parvus* Ditlevsen, 1904, were among the most abundant faunal species living in the aerenchyma of *Spartina* leaf sheaths, a microhabitat that supplies worms with food and oxygen and protection from predators (Healy & Walters 1993). The presence of aquatic Oligochaeta in plant aerenchyma has not previously been reported.

The three new species can all be referred to *Marionina* as defined by Nielsen & Christensen (1959). The genus was erected by Michaelsen (1989) to contain a group of species removed from *Pachydrilus*, but his di-

agnosis was inadequate to describe the new taxon. Černosvitov, in his review of the Enchytraeidae (1937), considered the systematic position of *Marionina* to be unclear but retained the taxon as a sub-genus of *Pachydrilus* in which he included 37 species. Nielsen & Christensen (1959) subsequently removed several species to other genera but admitted that *Marionina* remained heterogeneous. Their diagnosis is concerned entirely with negative or variable characters and there is, at present, no derived character that distinguishes the genus as a whole. *Marionina* species are recognized by their small size and the absence of characters that define other genera such as peptonephridia, intestinal diverticula, an anterior origin of the dorsal vessel, two kinds of coelomocytes, lobed seminal vesicles and setae with enlarged ental hooks. The genus has thus become a deposit for any small species that do not conform to other existing generic diagnoses. The 70 or so species currently included in *Marionina* constitute a heterogeneous assemblage comprising at least two lineages (Coates 1987, 1989) and some species of doubtful affinity (Nielsen & Christensen 1959; Coates 1980, 1987). Most of the marine species, however, form a homogeneous monophyly, characterized by an anterior bifurcation of the dorsal vessel in III or IV, i.e., posterior to the brain, instead of anterior to the brain as in most enchytraeids (Coates 1987, 1989, 1990). The three new species described in this paper fall into this group. They are distinguished from other marine *Marionina* by setal shape and number, the point of origin of the dorsal blood vessel, the form of the sperm funnel and development of the seminal vesicle and by characters of the spermatheca, including the arrangement of sperm in the ampulla.

Materials and Methods

Most of the material was collected in May, 1991 from the Kenan Field salt marsh on Sapelo Island (31°23'N, 81°17'W) where samples were taken from high and low marsh and creekside as part of an investigation into the microdistribution of Oligochaeta (Healy & Walters 1993). The substrate was silt and the salinity 20–30‰. A few samples containing one or more of the new species were also taken from *Spartina* marshes in other parts of Sapelo Island, and from marshes at two sites in N. Florida. The latter collections were part of a survey of intertidal and supratidal habitats in Georgia and east Florida in 1990 and 1991 (unpublished) which has provided information on the ecological limits of the species described in this paper.

Samples were taken from surface mud, roots and leaf debris and the lower stems of live and standing dead *Spartina* plants. Worms were extracted from mud by sieving and from plant material by a modified version of the wet-funnel method, using 100 W light bulbs to raise the temperature in the funnels over 40°C in 1–2 hours (Healy & Rota 1992). Leaf sheaths were shredded lengthwise before extraction. Specimens were fixed in 70% ethanol, stained in paracarmine and whole-mounted in Canada Balsam.

Type specimens and other material are deposited in the United States National Museum of Natural History, Washington, D.C. (USNM). Other whole mounts are in the collection of the University of Georgia Marine Institute, Sapelo Island (UGMI), or in the author's collection. All material was collected by the author.

Marionina spartinae, new species
Fig. 1

Material examined.—Holotype: USNM 163805, stained whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May 1991. Paratypes: USNM 163806–163807, stained whole mounted specimens from the type locality, May 1991. Other material from the type locality: USNM 163808–163812; UGMI two whole mounted specimens; 98

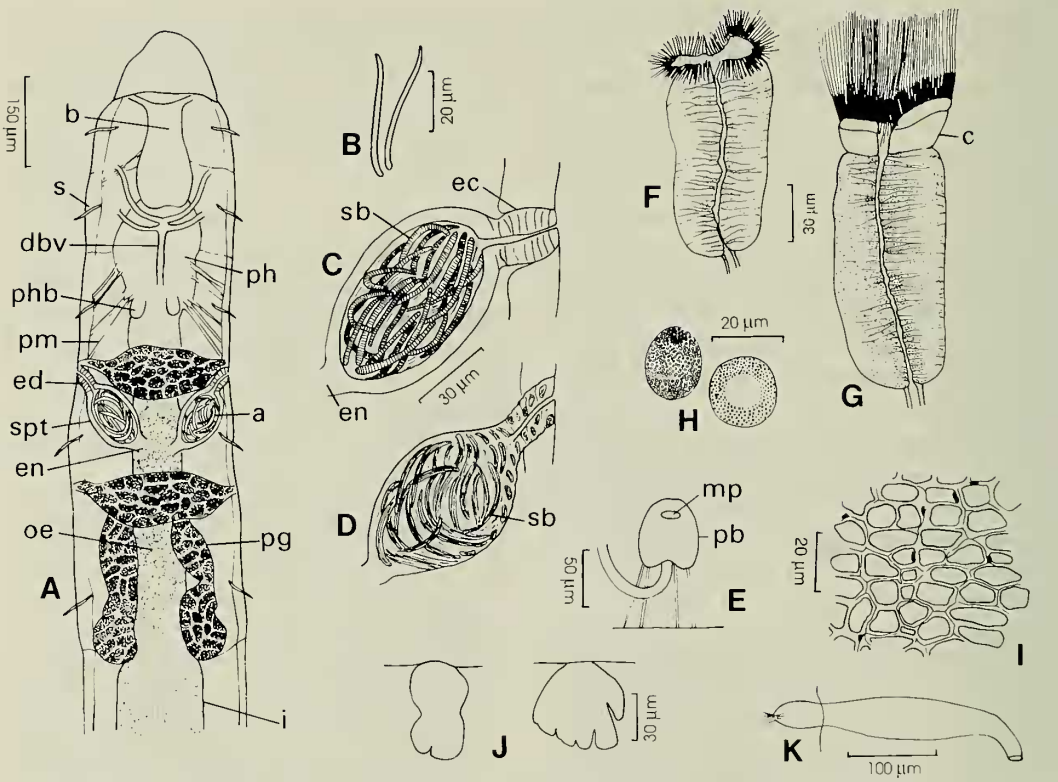

Fig. 1. *Marionina spartinae,* new species. A, schematic view of anterior region from combined observations on several fixed specimens; B, setal bundle; C, spermatheca of live specimen; D, spermatheca of fixed specimen; E, penial bulb; F, sperm funnel of fixed specimen; G, sperm funnel of live specimen; H, coelomocytes; I, clitellar glands; J, testes from two fixed, mounted specimens; K, nephridium at 8/9, live worm. a, ampulla; b, brain; c, collar of sperm funnel; dbv, dorsal blood vessel; ec, ectal duct; en, ental duct, i, intestine; mp, male pore; oe, esophagus with chloragocytes; pb, penial bulb; phb, pharyngeal bulb; pg, pharyngeal gland; ph, pharnyx; pm, pharyngeal muscles; s, setal bundle; sb, sperm bundle; spt, spermatheca.

whole mounted specimens in the author's collection. Approximately 25 live specimens examined.

Etymology.—The specific name refers to the salt marsh plant *Spartina* with which the species is almost exclusively associated.

Description.—Length of live worms 5–8 mm, width 0.27 mm at VII, 0.30 mm at the clitellum. Fixed, mounted specimens 4–5 mm long and 0.16–0.22 mm wide. Segments (22)26–32(42) (n = 130). Setae two per bundle in all segments and positions, usually absent in XII, sigmoid without ental hooks, 38–48 µm in the preclitellar region, 48–56 µm in posterior segments, of roughly equal length within a bundle (Fig. 1B). Cutaneous gland cells inconspicuous in live specimens but about three double rows may be seen in each segment in stained mounts. Clitellum extending over XII–½XIII, slightly raised, gland cells either in transverse rows, poorly developed, or irregular when well developed, absent mid-ventrally between the penial bulbs (Fig. 1I). Head pore in the middle of the prostomium.

Three pairs of pharyngeal glands, the first two united dorsally without ventral lobes, the third pair separate with elongated ven-

tral lobes and small dorsal lobes (Fig. 1A). A pair of bulbs present on the posterior border of the pharynx (Fig. 1A). Esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes forming a dense layer from V, 5–8 cells across the intestine, containing small, sparse droplets. Coelomocytes nucleate, round or oval, sometimes with small, blunt points, filled with refringent granules, the cells appearing gray or light brown by transmitted light in live worms, length 19–23 μm (Fig. 1H). Blood colorless. Dorsal vessel originating in the preclitellar region, usually at 9/10, occasionally at 10/11, anterior bifurcation in III (Fig. 1A). Brain about twice as long as its maximum width, 115–120 μm long, indented posteriorly (Fig. 1A). Nephridia starting at 7/8, the anteseptal part ovoid with coils of the canal surrounding the nephrostome, postseptale more or less cylindrical, the efferent duct terminal, short and stout (Fig. 1K).

Testes bulky, somewhat lobed (Fig. 1J), seminal vesicle unpaired, confined to XI or extending forward asymmetrically to X or 9/10. Sperm funnel half to two-thirds the diameter of the worm, about twice as long as wide in live worms (Fig. 1G), about 1.5 times as long in fixed specimens (Fig. 1F), with a tall, somewhat flared, asymmetrical collar to which abundant, dark-staining sperm are attached. The funnel has a granular appearance and in living worms has an irregular outline. Sperm duct stout, 7–12 μm in diameter, of medium length, opening at a small, compact penial bulb, maximum diameter 25–37 μm. One to three mature eggs present at a time. Spermathecal ampulla ovoid, about twice as long as wide, 60–80 μm × 40–55 μm, thick-walled in live specimens, the wall not easily distinguishable in stained mounts, containing elongated sperm bundles (Figs. 1C, D). In live worms, the bundles are transversely striated, but striations are hard to see in stained mounts. Ectal duct short, only about 1.5 times the thickness of the body wall, without separated, projecting gland cells. Ental duct broad and short, thick-walled, uniting with the esophagus at about the level of the setae in V (Fig. 1A).

Remarks.—The distinctive characters of *M. spartinae* are its paired, sigmoid setae, the preclitellar origin of the dorsal vessel and the unusual arrangement of sperm in the spermathecal ampulla. Only a few species of *Marionina* are described as having distinctly sigmoid setae and none of these have paired setae in all segments. An anteclitellar origin of the dorsal vessel at 8/9 or in IX is unusual in *Marionina* and has only been reported for three terrestrial species from S. America: *M. ecuadoriensis* Righi, 1981, which has free spermathecae, i.e., not attached to the esophagus; *M. cana* Marcus, 1965, which has straight setae; and *M. nea* Marcus, 1965, which has 2–5 slightly sigmoid setae. In other species the origin is intraclitellar or postclitellar. The arrangement of sperm in elongated bundles in the spermatheca is unique in the Enchytraeidae, although in *Grania* and in several species of *Marionina* there are spherical sperm bundles. The bundles differ from similar shaped bundles found in some Tubificidae (Baker & Brinkhurst 1981, Erséus 1982) in lacking an outer hyaline layer which, as shown by Braidotti et al. (1980), is formed by helically wound, modified spermatozoa with degenerate nuclei and which surrounds a core of fertilizing spermatozoa. The cross striations seen in the bundles of *M. spartinae* suggest a different arrangement, but electron microscopic studies would be needed to elucidate the structure.

Habitat.—*Spartina* salt marshes, chiefly in the leaf sheaths of live and standing dead *Spartina* plants, less frequently in surface mud and decaying plant debris. One record from plant debris at the edge of a brackish lake, salinity 22‰.

Distribution.—Common and widespread

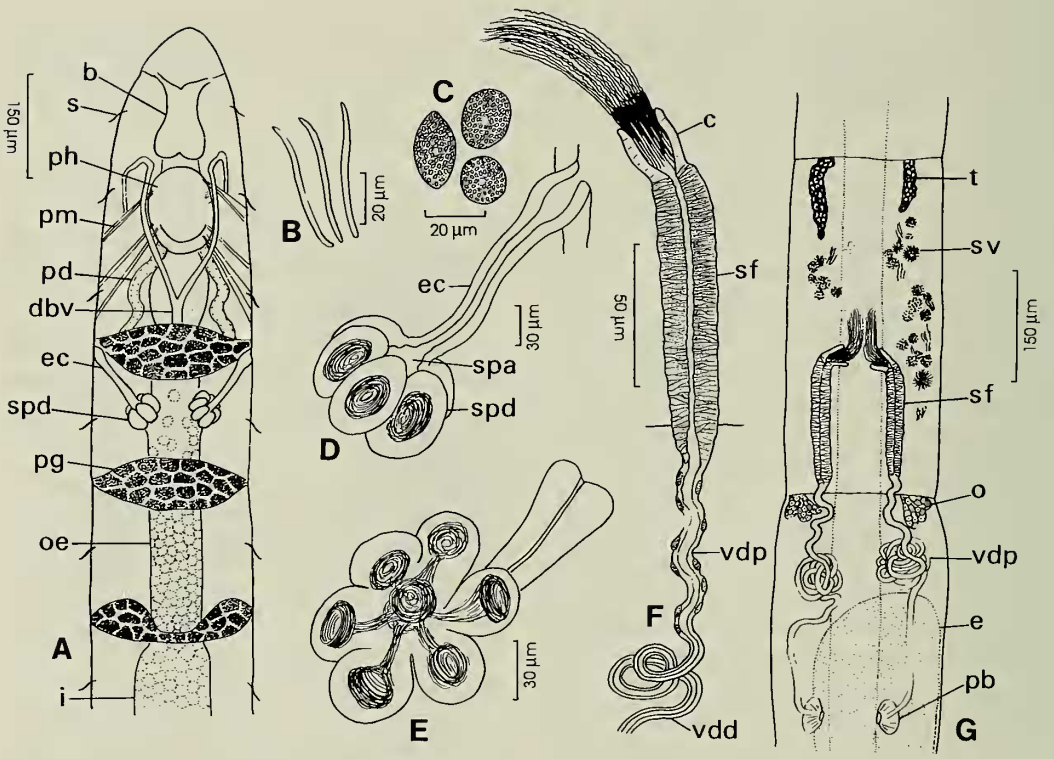

Fig. 2. *Marionina waltersi,* new species. A, schematic view of anterior region from combined observations on several fixed specimens; B, setal bundle; C, coelomocytes; D, spermatheca of live specimen; E, spermatheca of fixed specimen; F, sperm funnel and part of duct in live specimen; G, segments XI and XII. b, brain; c, collar of sperm funnel; dbv, dorsal blood vessel; e, egg; ec, ectal duct; i, intestine; o, ovary; oe, esophagus with chloragocytes; n, nephridium; pb, penial bulb with male pore; pd, duct of pharyngeal glands; pg, pharyngeal gland; pm, pharyngeal muscle; s, setal bundle; sf, sperm funnel; spa, spermathecal ampulla; spd, spermathecal diverticulum; sv, seminal vesicle, poorly defined; vdd, distal part of vas deferens; vdp, proximal part of vas deferens.

on Sapelo Island; Guana Lake, near St. Augustine, Florida.

Marionina waltersi, new species
Fig. 2

Material examined.—Holotype: USNM 163813, stained, whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May 1991. Paratypes: USNM 163814–163815, stained, whole mounted specimens from the type locality, May 1991. Other material: UGMI, one stained, whole mounted specimen; 25 stained whole mounts in the author's collection. Approximately 16 live specimens examined.

Etymology.—The species is named for Dr. Keith Walters, meiofaunal specialist at the Marine Institute, Sapelo Island, who first drew my attention to the presence of enchytraeids in *Spartina* stems.

Description.—Live worms 5–6.5 mm, width 0.22 mm in the preclitellar region, 0.27 mm at the clitellum. Fixed, mounted specimens 3–4 mm long and 0.16–0.24 mm wide. Segments (21)25–29(35) (n = 25). Setae slightly sigmoid without ental hooks (Fig. 2A), (2)3(4) in preclitellar segments, 2–3 be-

hind the clitellum, 43–56 μm anteriorly, 48–60 μm in posterior segments. Within a bundle, the outer setae are 4–6 μm longer than those near the midline. Cutaneous gland cells not apparent. Clitellum extending over XII–¾XIII, gland cells more or less in transverse rows near anterior and posterior borders, arranged irregularly in the central zone, gland cells present in the mid-ventral region. Head pore near the middle of the prostomium.

Three pairs of pharyngeal glands, the first two broadly united dorsally, the third united by a narrow band of tissue, all without ventral lobes (Fig. 2A). Pharyngeal and esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes present from V, forming a dense layer from VI, about 5–6 cells across the intestine, containing fine droplets. Coelomocytes oval, 19–25 μm, one-half to one-third the length of the setae, with coarse and small granules, appearing gray or light brown by transmitted light in living worms (Fig. 2C). Blood colorless. Dorsal vessel originating at 12/13, in XIII or at 13/14, anterior bifurcation in III or IV. Brain about 1.3–1.4 times as long as broad (fixed, mounted material), slightly indented. Nephridia starting at 7/8 or 8/9, anteseptale ovoid with coils of the canal surrounding the nephrostome, postseptale more or less cylindrical, slightly more swollen than in *M. spartinae,* efferent duct terminal, short and stout.

Testes small, unlobed, elongate, sometimes extending from 10/11 to mid XI. Seminal vesicles poorly developed (Fig. 2G) or absent. Sperm funnel long and narrow, five to six times as long as wide, roughly equal in length to the diameter of the worm (Fig. 2F). A tall, funnel-shaped collar is usually bent towards the midline while the funnel itself is straight or slightly sinuous, tapering distally as it passes through 11/12 to form a thin-walled, sinuous duct with isolated cells on its surface, about half as long as the funnel (Fig. 2F). The sinuous duct, which represents the proximal region of the vas deferens, is followed by a long, narrow, much-coiled distal region, confined to XII (Fig. 2G). Sperm attached to the funnel notably long and wavy (Fig. 2F). Penial bulb compact, 42–48 μm in diameter. One or two mature eggs present at a time. Spermathecal ampulla surrounded by a ring of five or six, more or less spherical, thick-walled diverticula on short stalks (Figs. 2D, E). Sperm present in the central chamber, in the radiating canals and in rings in the bulbous chambers of the diverticula. In live worms, the rings of sperm often rotate. Ental duct very short, the ampulla apparently closely applied to the lateral wall of the esophagus at about the level of the setae in V (Fig. 2A). Ectal duct thick-walled, about 15 μm in diameter, with a narrow canal, 2.5 times the length of the ampulla, swelling slightly near its opening where there may be a small narrow chamber.

Remarks.—*Marionina waltersi* resembles *M. southerni* (Černosvitov, 1937 pro *Enchytraeus lobatus* Southern, 1909) in having a ring of sperm-containing diverticula around the spermathecal ampulla but in *M. southerni* these are sessile and more numerous, there is a rosette of glands surrounding the orifice of the ectal duct, the seminal vesicle is large, the sperm funnel thick, the coelomocytes are dense and the paired setae are straight. *Marionina southerni* has been recorded in Massachusetts and North Carolina (Lasserre 1971). The only other *Marionina* for which a ring of spermathecal diverticula has been described is the poorly known *M. georgiana* (Michaelsen 1888) from the Antarctic, which is a larger species (around 35 segments), has up to 6 setae per bundle and a funnel only twice as long as broad. The long, narrow sperm funnel of *M. waltersi,* followed by a duct in two sections of different thickness has not been described for any other species of *Marionina.*

Habitat.—In *Spartina* salt marshes, in plant stems and occasionally in surface plant

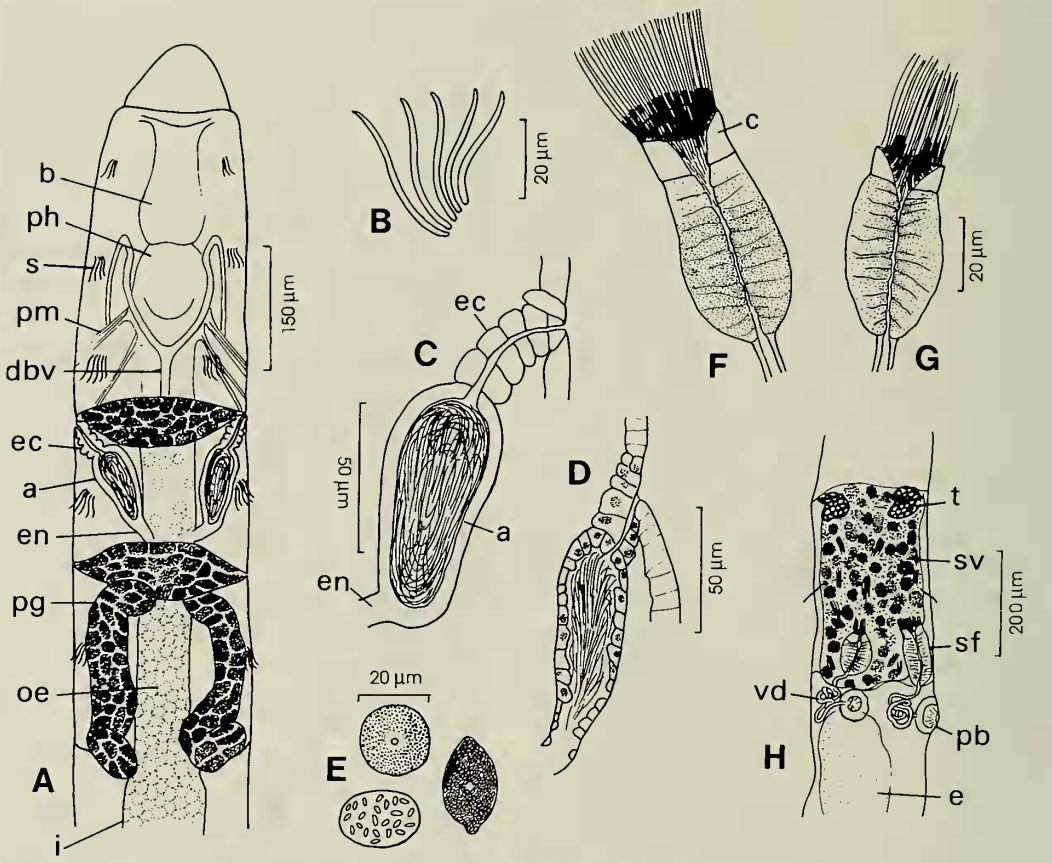

Fig. 3. *Marionina paludis,* new species. A, anterior region; B, setal bundle; C, spermatheca of live specimen; D, spermatheca of fixed specimen; E, coelomocytes; F, sperm funnel of live specimen; G, sperm funnel of fixed specimen; H, segments XI and XII. a, spermathecal ampulla; b, brain; c, collar of the sperm funnel; dbv, dorsal blood vessel; e, egg; ec, ectal duct; en, ental duct; i, intestine; oe, esophagus with chloragocytes; pb, penial bulb; pg, pharyngeal gland; ph, pharynx; pm, pharyngeal muscle; s, setal bundle; sf, sperm funnel; sv, seminal vesicle; vd, vas deferens.

debris. One record from the edge of a brackish lake, 22‰.

Distribution.—Sapelo Island, Georgia; Guana Lake, near St. Augustine, Florida.

Marionina paludis, new species
Fig. 3

Material examined.—Holotype: USNM 163816, stained, whole mounted specimen, Kenan Field salt marsh, Sapelo Island, May, 1991. Paratypes: USNM 163817–163818, two stained, whole mounted specimens from the type locality, May 1991. Other material: UGMI, three stained whole mounted specimens from the type locality; 18 whole mounted specimens from several marshes on Sapelo Island in the author's collection. Approximately 20 live specimens examined.

Etymology.—From the Latin *palus*—a marsh, because the species is associated with salt marsh habitats.

Description.—Live worms 4–6 mm, width 0.18–0.21 mm, 0.24–0.28 mm at the clitellum. Fixed, mounted specimens 3.5–4.5 mm long and 0.13–0.26 mm wide. Segments (21)24–28 (n = 25). Setae sigmoid, without

ental hooks, usually 3–6 per bundle, (2–3)4(5) laterally and 4–6(7) ventrally in the preclitellar region, 3–4 laterally and 4–5 ventrally behind the clitellum. Setae are arranged fanwise within a bundle, those near the midline being smaller than the outer zones with a stronger curvature (Fig. 3B), size range 28–46 μm in the preclitellar region, 40–46 μm in posterior segments. Cutaneous gland cells variable, inconspicuous or in 3–8 rows of transversely elongated cells per segment. Sometimes the cells are fused to form a continuous, irregular line up to half the diameter of the worm which may possess small branches. Clitellum over XII–½XIII, clitellar gland cells irregularly distributed, absent ventrally in most specimens. Head pore at 0/1.

Three pairs of pharyngeal glands, the first two pairs broadly united dorsally without ventral lobes, the third pair free with long ventral lobes and small dorsal ones (Fig. 3A). Pharyngeal and esophageal diverticula absent. Esophagus merging gradually with the intestine from 6/7. Chloragocytes forming a dense layer from VI, 5–6 cells across the intestine. Coelomocytes mainly oval, some with small blunt points, occasionally round, 19–24 μm i.e., about two-thirds the length of anterior setae, with small granules, appearing gray or light brown by transmitted light in live worms. Blood colorless. Dorsal vessel originating at 12/13 or in XIII, anterior bifurcation at around 3/4. Brain about 1.5 times as long as wide in fixed worms, slightly indented posteriorly. Nephridia starting at 6/7, similar to those of *M. spartinae.*

Testes more or less globular, not or only slightly lobed (Fig. 3H). Seminal vesicle unpaired, confined to XI (Fig. 3H). Sperm funnel cylindrical, confined to XII, twice as long as broad, 80 × 40 μm in live worms, about half the diameter of the worm (Figs. 3F, G). Sperm duct of medium length, penial bulb compact, 30 μm in diameter. Usually only one mature egg present at a time. Spermathecal ampulla cylindrical or cone-shaped, with a rather thick wall (Figs. 3C, D), united with the lateral esophageal wall in the posterior part of V (Fig. 3A). Ectal duct about half as long as the ampulla, covered with a layer of rounded cells (Figs. 3C, D).

Remarks.—*Marionina paludis* closely resembles *M. appendiculata* Nielsen & Christensen, 1959 in size and general anatomy, especially in having fan-like bundles of 4–7 sigmoid setae. It differs in its much larger spermathecal ampulla with shorter ectal duct covered in a layer of large cells, in its larger sperm funnel, larger rounded testes and the presence of a well developed seminal vesicle and compact penial bulb. *Marionina appendiculata* is characteristic of muddy substrates in marine and estuarine littoral zones and is present on the Sapelo marshes. It is a widespread species and, as currently recognized, displays some variations in the size of the sperm funnel, in the development of the seminal vesicle and in the organs associated with the male pore. Some variants may indeed prove to be distinguishable as separate species. In North American material from western Canada (Coates & Ellis 1981) and from Georgia and both Atlantic and Gulf coasts of Florida (pers. obs.) the sperm funnel is always small, usually only 0.25 the diameter of the worm, the testis is small (elongated in Sapelo specimens), a seminal vesicle is absent and there are one or two free glands at the male pore which are occasionally fused around the opening. Where the species occur together, therefore, *M. paludis* can be recognized by its larger sperm funnel, larger, rounded testes and well developed seminal vesicle and penial bulb, even when the spermatheca is not clearly distinguished. Immature specimens are difficult to separate although *M. appendiculata* is generally smaller, with somewhat smaller and finer setae which may reach eight per bundle.

Habitat.—*Spartina* marshes, chiefly in standing dead stems, less frequently in plant

debris on the marsh surface and in live stems of creekside *Spartina*.

Distribution.—Sapelo Island, Georgia.

Discussion

The three new species here described were common throughout the Sapelo marshes, *Marionina spartinae* being dominant. They were accompanied in all microhabitats except tidal debris by *M. appendiculata* and on the banks of creeks by immature *Enchytraeus*. No other enchytraeid species were found on the marshes. Two of the new species were also present at a *Spartina* marsh in N. Florida. A variety of other intertidal and supralittoral habitats have been investigated on the S. Georgia and N. Florida coasts, including *Salicornia* marshes, seagrass and other tidal debris, and plant roots near high water mark on the open coast. Other species of *Marionina* were found in these habitats but the new species appear to be confined to *Spartina* marshes.

Acknowledgment

Support for my visit to Sapelo Island was provided by the University of Georgia, Sapelo Island Research Foundation in the Marine Institute's Visiting Scientist Program. This is contribution No. 733 of the University of Georgia Marine Institute.

Literature Cited

Baker, H. R., & R. O. Brinkhurst. 1981. A revision of the genus *Monopylephorus* and redefinition of the subfamilies Rhyacodrilinae and Branchiurinae (Tubificidae: Oligochaeta).—Canadian Journal of Zoology 59:939–965.

Braidotti, P., M. Ferraguti, & T. P. Fleming. 1980. Cell junctions between the spermatozoa flagella within the spermatozeugmata of *Tubifex tubifex* (Annelida: Oligochaeta).—Journal of Ultrastructure Research 73:299–309.

Černosvitov, L. 1937. System der Enchytraeiden.—Bulletin de l'Association suisse pour les Recherches scientifiques à Prague 5:263–294.

Coates, K. A. 1980. New marine species of *Marionina* and *Enchytraeus* (Oligochaeta, Enchytraeidae) from British Columbia.—Canadian Journal of Zoology 58:1306–1317.

———. 1983. A contribution to the taxonomy of the Enchytraeidae (Oligochaeta). Review of *Stephensoniella* with new species records.—Proceedings of the Biological Society of Washington 96:411–419.

———. 1987. Phylogenetic analysis of some Enchytraeidae (Annelida: Oligochaeta): parsimony analysis of structural changes. Unpublished PhD thesis, University of Victoria, Canada.

———. 1989. Phylogeny and origins of Enchytraeidae.—Hydrobiologia 180:35–45.

———. 1990. Marine Enchytraeidae (Oligochaeta, Annelida), of the Albany area, Western Australia. Pp. 13–41, *in* F. E. Wells, D. I. Walker, H. Kirkman & R. Lethbridge, eds., Proceedings of the third international marine biological workshop: the marine flora and fauna of Albany, Western Australia. Western Australian Museum, Perth.

———, & D. V. Ellis. 1981. Taxonomy and distribution of marine Enchytraeidae (Oligochaeta) in British Columbia.—Canadian Journal of Zoology 59:2129–2150.

Erséus, C. 1982. Taxonomic revision of the marine genus *Limnodriloides* (Oligochaeta: Tubificidae).—Verhandlungen naturwissenschaftlichen Vereins in Hamburg, NF 25:207–277.

Giere, O. 1974. *Marionina istriae* n. sp., ein mariner Enchytraeide (Oligochaeta) aus dem mediterranean Hygropsammal.—Helgoländer wissenschaftliche Meeresuntersuchungen 26:359–369.

———. 1979. Studies on marine Oligochaeta from Bermuda, with emphasis on *Phallodrilus* species (Tubificidae).—Cahiers de Biologie marine 20: 301–314.

Healy, B. 1989. Preliminary report on the Enchytraeidae (Oligochaeta) of West Florida.—Hydrobiologia 108:47–56.

———, & E. Rota. 1992. Methods for collecting Enchytraeidae during expeditions.—Soil Biology and Biochemistry 24:1279–1281.

———, & K. Walters. 1993. Oligochaeta in *Spartina* stems: the microdistribution of Enchytraeidae and Tubificidae in a salt marsh, Sapelo Island, U.S.A.—Hydrobiologia (in press).

Lasserre, P. 1971. The marine Enchytraeidae (Annelida, Oligochaeta) of the eastern coast of North America with notes on their geographical distribution and habitat.—Biological Bulletin of the Marine Biological Laboratory, Wood's Hole 140: 440–460.

———, & C. Erséus. 1976. Oligochètes marins des Bermudes. Nouvelles éspèces et remarques sur la distribution géographique de quelques Tubificidae et Enchytraeidae.—Cahiers de Biologie marine 17:447–462.

Marcus, E. 1965. Naidomorpha aus brasilianischem Brackwasser.—Beiträge zur neotropischen Fauna 4:61–83.

Michaelsen, W. 1988. Die Oligochaeten von Sud-Georgien nach der Ausbeute der deutschen Station von 1882–1883. Jahrbuch Hamburger wissenschaftlichen Austatten 5:53–73.

———. 1889. Synopsis der Enchytraeiden.—Abhandlungen des naturwissenschaftlichen Vereins zu Hamburg 11:1–60.

Moore, J. P. 1902. Some Bermuda Oligochaeta with a description of a new species.—Proceedings of the Academy of Natural Sciences of Philadelphia 54:80–84.

———. 1905. Some marine oligochaeta of New England.—Proceedings of the Academy of Natural Sciences of Philadelphia 57:373–399, Plates 22–23.

Nielsen, C. O., & B. Christensen. 1959. The Enchytraeidae. Critical revision and taxonomy of European species.—Natura jutlandica 8–9:1–160.

Reimold, R. J. 1977. Mangals and salt marshes of eastern United States. Pp. 157–166 *in* V. J. Chapman, ed., Ecosystems of the world. 1. Wet coastal ecosystems. Elsevier Scientific Publishing Co., Amsterdam.

Righi, G. 1981. Alguns Oligochaeta cavernicolas do Equador.—Papéis Avulsos de Zoologia 34:235–249.

Southern, R. 1909. Contributions towards a monograph of the British and Irish Oligochaeta.—Proceedings of the Royal Irish Academy 27B: 119–182.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia.—Ecology 43:614–624.

Wiegert, R. G., L. R. Pomeroy, & W. J. Wiebe. 1981. Ecology of salt marshes: an introduction. Pp. 3–19 *in* L. R. Pomeroy and R. G. Wiegert, eds., The Ecology of a salt marsh. Springer-Verlag, New York.

Welch, P. S. 1917. The Enchytraeidae (Oligochaeta) of the Wood's Hole region, Mass.—Transactions of the American Microscopical Society 34: 119–138.

Department of Zoology, University College, Belfield, Dublin 4, Republic of Ireland.